Analysis of species attributes to determine dominant environmental drivers, illustrated by species decline in the Netherlands since the 1950s

C.J.M. Musters*, Peter M. van Bodegom

Institute of Environmental Sciences, Leiden University, P.O. Box 9518, 2300 RA Leiden, The Netherlands

ARTICLE INFO

ABSTRACT

The relative impact of climate change and land use change on biodiversity loss is still under discussion. To alleviate drawbacks related to the use of observed species distributions, we introduce a novel approach to separate the effects of climate change and land use change, the latter split into fragmentation, agricultural intensification and reforestation.

This approach, coined the Attribute Importance Analysis (AIA), uses the ability of species attributes to explain population declines. Through the a priori association between attributes and individual drivers, the relative importance of the drivers in causing the species decline can be assessed. We tested this approach on the population decline of vertebrate, insect, vascular plant, and fungi species in the Netherlands since the 1950s.

Fragmentation was clearly the strongest driver of species decline for vertebrates and plants, and this may also be true for insects. For fungi, climate change seems the only driver. We found a weak signal of the importance of agricultural intensification for the decline of vertebrates only. We ascribe this unexpected low importance of agricultural intensification to our partitioning of agricultural effects into fragmentation and intensification.

Our generic approach can offer valuable quantitative information on the relative importance of drivers that change local community composition without the need for spatial explicit information. Without data on temporal trends in drivers, including local climate and land use change, accurate information on species decline, species attribute values and association of attributes with drivers can give insights into the causes of species decline, which, in turn, can be used to adapt nature management accordingly.

1. Introduction

In the Millennium Ecosystem Assessment (2005), land use change is regarded as the most important driver, in the sense that the observed biodiversity loss is considered as mainly the result of habitat loss. Climate change is the driver that, together with pollution, is expected to have a large impact on biodiversity in the near future (MEA, 2005). However, the relative importance of climate change versus land use changes as the main drivers of biodiversity change is presently under discussion, while crucial for developing general conservation strategies and implementation plans (Fox et al., 2014; Bradshaw et al., 2015; Urban, 2015; Fraixedas et al., 2015; Elmhagen et al., 2015a; Lehsten et al., 2015). Feeding this discussion with traditional empirical data is difficult, because one needs long term data on biodiversity change in an area that is large enough to include a gradient of climate change as well as a similar gradient of land use change in which the correlation between climate change and land use change is not so strong that the statistical separation of the two impacts is impossible. Although such

data are available for certain plant and animal groups for specific areas, such as British birds (Bradshaw et al., 2015) and moths (Fox et al., 2014) or birds in Finland (Luoto et al., 2007; Fraixedas et al., 2015), finding accurate information for clarifying the relative importance of drivers across different high-level taxonomic groups is extremely difficult at present.

We propose an alternative, trait-based approach for analyzing the decline of species, which does not have such data requirements and that can be applied to directly compare different taxonomic groups. Such an approach is possible because ecological traits are supposed to reflect the ecological strategies of species in relation to and in interaction with environmental drivers (Violle et al., 2007; Webb et al., 2010; Murray et al., 2011; Angert et al., 2011; Mouillot et al., 2013: van Bodegom et al., 2014). We assume that a change in a local environmental driver results in the selection in the community sensu Vellend (2016): some species will become less abundant and others will thrive, depending on their trait values. Recently, traits were used to show selection by land use change, climate change, and change in nitrogen deposition,
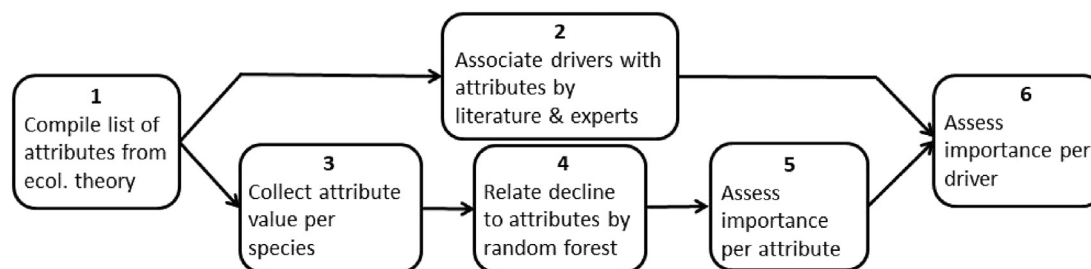

Fig. 1. Procedure of Attribute Importance Analysis (AIA). The six steps are further explained in 2.2.

respectively (Bregman et al., 2017; Siepielski et al., 2017; Bowler et al., 2017; van Strien et al., 2017; Pöyry et al., 2017). In other words, when a specific driver changes the environment, only those species that have a particular combination of trait values will decline. If this is true, we can, in principle, use the trait values of declining species to study which environmental drivers are responsible for the decline.

To implement this concept, we developed an approach based on decision trees that we call the Attribute Importance Analysis (AIA). We use the word 'attribute' instead of 'trait' in line with the literature on decision trees. AIA is a strict a priori approach in the sense that we first hypothesize which attributes should have a high predictive power for decline, given a particular driver, and then use the actual predictive power of the attributes to test this.

Here, we provide a proof of principle and use AIA by applying it to assess the relative effect of four environmental drivers on species decline since the 1950s as reported in the Dutch red lists (Kalkman et al., 2010; Wamelink et al., 2013; CBS, PBL, and Wageningen UR, 2014). The first driver is climate change. The other three are different aspects of land use change: i) fragmentation, which reflects isolation of natural areas; ii) agricultural intensification, which reflects the change in land use intensity in cultivated areas; and iii) reforestation, which reflects the resent increase of wooded area in the Netherlands both in cultivated and natural areas. We separately analyzed four widely different species groups - vertebrates, insects, plants and fungi - for which we have data sets of many species and their attributes.

2. Materials and methods

2.1. Species and decline

In the Netherlands, Red lists are available for vertebrates, for insects belonging to Plecoptera, Orthoptera, Ephemeroptera, Odonata, Lepidoptera, Trichoptera, and Apidae, for plants belonging to the vascular plants, bryophytes and lichens, and for a large number of fungi with visible fruiting bodies (mushrooms) (Supplementary material, Appendix A). These can be regarded as representative for above-ground terrestrial and freshwater macro-species within the Dutch territory, while small species, marine species and soil species are under-represented (Noordijk et al., 2010; Musters et al., 2013).

To obtain a balanced representation of the high level taxa within each of our species groups, we randomly selected a similar number of species per taxon. From taxa with only a few species, e.g., reptiles, we selected all species (for details see Musters et al., 2013). In total, we selected 175 vertebrate species (out of a total of 297 species), 371 insect species (out of 724 species), 303 plants (out of 2513 species) and 249 fungi (out of 2405 species) from the Red lists.

Red lists evaluate the threat state of a species based on both its rarity and observed decline. The background documentation of the Red lists assesses the decline of the species based on real observations only. The categories used to indicate the trend ('stable or inclining', 'not declining', 'moderately declining', etc.) are standardized and equal for all species groups. We defined decline as a binary variable indicating whether or not the species range or abundance has been declining in the

Netherlands since the 1950s (categories 'moderately declining', 'strongly declining', 'very strongly declining' and 'maximally declining/ extinct'; de Iongh and Bal, 2007; Musters et al., 2013). Declining species occur in any of the Red list categories, from least concerned to critically endangered. Of our selected vertebrates, 44% are in our definition declining, as are 52% of the insects, 29% of the plants and 46% of the fungi.

2.2. Attribute Importance Analysis

The Attribute Importance Analysis (AIA) consists of six steps. First, based on ecological theory, we compiled a list of all attributes that may be related to the vulnerability of species to environmental change (box 1 in Fig. 1). Second, we postulated how each environmental driver of interest is associated with each attribute in the sense that the value of that particular attribute would affect the abundance or the reproduction rate of species. Thus for each driver, we compiled a set of attributes that is associated with that driver (box 2). Third, we collected information on the attributes values of the species in our study (box 3). Fourth, we explained the decline of species from their attribute values using a machine learning technique based on decision trees, i.e., random forests (box 4). Fifth, the explanatory power of the attributes was assessed by estimating the 'importance' of the attributes in explaining the decline of species by the random forest (box 5). And sixth, we aggregated the importance of the sets of attributes associated with individual drivers (from box 2) to assess which environmental drivers are likely the most important for the decline of species. We calculated two different metrics for this: the *proportion* of attributes associated with a specific driver that had the ability to explain the species decline and the *mean* importance of the same set of associated attributes. As part of our sixth step, we tested whether these two metrics significantly deviated from a random sample of attributes (box 6). To summarize, the list of associated attributes can be regarded as a set of hypotheses. Then we calculate which attributes are actually explaining decline accurately. If many of these accurate predictors are in the set of hypotheses, we regarded that as supporting the idea that the driver is an important driver. Below we describe the six steps of AIA more extensively.

2.2.1. Compile list of attributes

To identify attributes associated with the decline of species across taxonomic groups, we used the published list of 'universal' factors of decline from Musters et al. (2013). This list covers all aspects of life history based on ecological theory (Appendix B, Table B1). The list of factors was translated into a list of 128 attributes (Table B2).

2.2.2. Associate drivers with attributes

Environmental drivers were associated to attributes based on the framework that Williams et al. (2008) developed for assessing the vulnerability of species to climate change. We generalized this framework by deleting the references to climate change and made a distinction between the vulnerability to fragmentation as such, and the other drivers, that could have indirect fragmentation effects (Fig. 2). We used literature (Appendix C, Table C1) and expert knowledge to
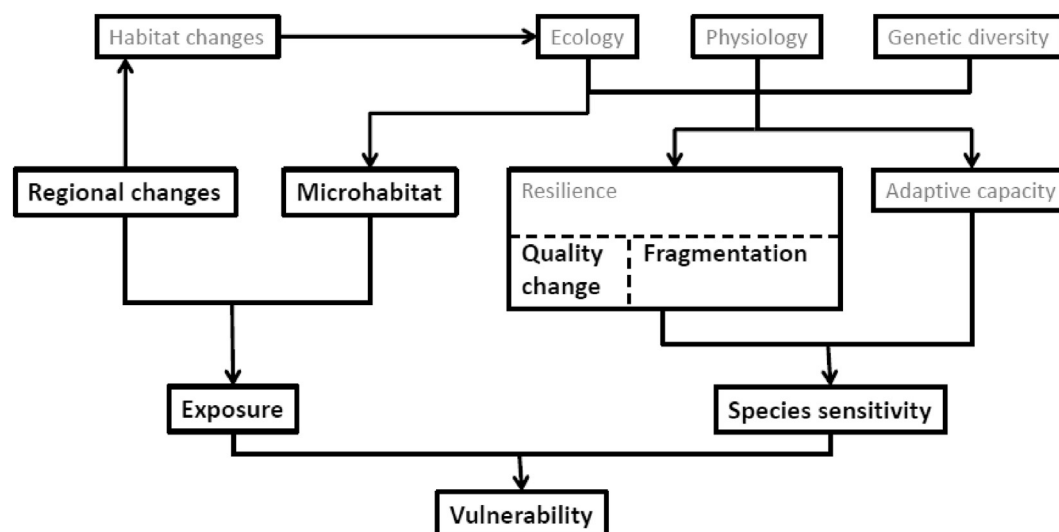
Fig. 2. General framework to assess the vulnerability of species to drivers of change. For associating attributes to individual drivers we used the bold categories. Adapted after Williams et al. (2008).

evaluate attributes related to landscape (*regional changes* in the framework) and local habitat (*microhabitat*) – together these are classed as *exposure* attributes. Attributes related to sensitivity to *quality change* and *fragmentation* were classed as *species sensitivity*. We excluded attributes that could affect the vulnerability of species to all four drivers, such as 'adaptive capacity'. By doing so, we simplified Williams et al.'s framework to the bold categories in Fig. 2. An overview of the selected attributes per driver is given in Table 1. For more extensive information on the procedure and references see Appendix C.

Climate change is our first driver. Changes in species distribution and phenology that can be attributed to climate change are common in the Netherlands and are usually assumed to have started in the 1980s (e.g., Kleukers and Reemer, 2003; Visser and Both, 2005; Dingemans and Kalkman, 2008; Tamis et al., 2009; Kalkman et al., 2010; Musters et al., 2010; Wereld Natuur Fonds, 2015). In total 32 attributes were associated with climate change. Some of these attributes indicate the species sensitivity to weather (temperature, humidity and wind). Climate change may affect the phenology of species, which can result in asynchrony between a species and the species on which it depends, particularly affecting specialist species. Also, those attributes that reflect global range margins and known shifts of these margins were included.

Fragments of natural areas are usually small and isolated in the Netherlands in a landscape of mainly urbanized and cultivated land, and can be regarded as the end result of large land use changes that occurred over the past centuries. While most loss of natural areas has stopped after WWII, dispersal barriers have increased because of intensification of land use (e.g. agriculture), disappearance of semi-natural elements such as ponds and hedgerows, and growth of urban areas, road length and traffic (Wamelink et al., 2013; CBS, PBL, and Wageningen UR, 2014; Wereld Natuur Fonds, 2015). So, since the 1950s, fragmentation of natural areas in the Netherlands implies increased isolation (fragmentation sensu stricto; Fahrig, 2003). We associated 33 attributes with fragmentation. These are related to species depending mainly on natural areas. For colonization ability, attributes related to dispersal ability, the number of offspring, and abundance were selected. Success in colonization may also be limited by dependence on specific other species.

Dutch agriculture started to intensify in the 1850s with major intensifications since the 1950s and is now among the most intensive of the world, while production per ha is still increasing (Stoate et al., 2009; Geiger et al., 2010). We associated 23 attributes with agriculture intensification, of which a number relate to species occurrence in early

successional stages and nutrient availability. Since water availability is manipulated in agriculture, an attribute related to humidity was included, as well as those that are related to human disturbance.

In a number of areas, woodlots have recently been planted, especially around the large cities of the western part of the Netherlands. Moreover, both in natural and cultivated areas, the cover of trees and bushes is increasing, at least since the 1980s (CBS, PBL & Wageningen UR, 2008 & 2014; Wereld Natuur Fonds, 2015). In the natural areas, the increase of trees and bushes took place at the cost of open areas like heath lands and moors (CBS, PBL, and Wageningen UR, 2013). We have called this process 'reforestation' because of a lack of a more appropriate term. With reforestation 18 attributes were associated, specifically those related to environmental conditions of forests, such as shadiness, shelter and humidity, but also the dependency on dead wood.

2.2.3. Collect attribute value per species

The attribute values per species were obtained by asking at least one expert to provide the attribute values of 'their' species group. These values were then checked for consistency and obvious errors by the Naturalis Biodiversity Center, Leiden, The Netherlands. Obviously, not all attributes are relevant for all species groups. For both vertebrates and insects there were 87 attributes, for plants 42 and for fungi 30 attributes (Table B2).

All attributes were transformed into categorical variables in order to avoid the influence of cardinality on the importance of attributes (Deng et al., 2011). In the case of scale variables, the scale-axis was divided into five equal parts, leading to a five-point ordinal attribute. When needed, the original values were log-transformed to approach a normal distribution before transforming into an ordinal attribute.

2.2.4. Explain decline based on attributes: random forests

We used random forests to evaluate the power of attributes to explain the demographic decline of species. Random forests consist of a large number of decision trees (Breiman, 2001). In our case, these were classification trees that classify the species as either declining or not. Each tree uses a random sample of species and attributes as a learning set. Using a random forest instead of a single classification tree prevents over-fitting (Breiman, 2001; Strobl et al., 2009). Random forests are especially fit for handling datasets in which the number of predictive variables (here attributes) is large compared to the number of cases (here species) (Strobl et al., 2009). They do not have a problem with handling non-linear relationships between the predictive variables and
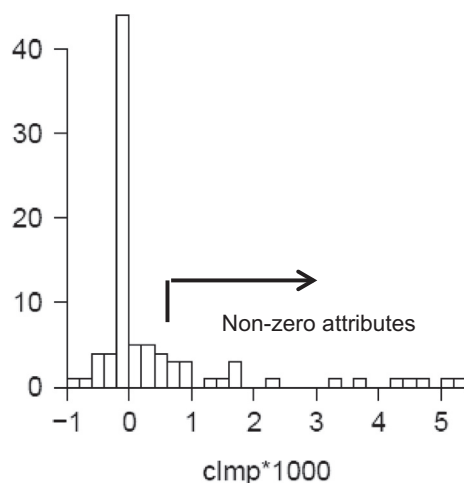
Table 1

Classification of the attributes based on species exposure and sensitivity following the adapted framework from Williams et al. (2008) (in rows) as associated with climate change and land use change drivers (in columns). Numbers refer to attribute numbers of S1.

		Climate change	Fragmentation	Agricultural intensification	Reforestation

Exposure	Regional change	Global range margins
		  11: Margin through the Netherlands
		  13: Margin shift 1900–1990
		  14: Margin shift since 1990
			Nature areas
			  19: Dependence on natural habitats
			  20: Preference for urban or agricultural habitats
				Agricultural areas
				  15b: Main habitat freshwater
				  19: Dependence on natural habitats
				  20a: Preference for agricultural areas
				  21: Preference habitat stability
					Terrestrial areas
					  15: Main habitat

	Micro-habitat	Temperature
		  37a: Endotherm
		Humidity
		  17: Terrestrial humidity
		Wind
		  52b: Pollination by wind
		  53a: Seed dispersal by wind
				Early succession stages
				  16: Forest or non-forest habitats
				  50: Shadiness growing habitat
				Humidity
				  17: Terrestrial humidity
				Nutrients
				  61: Nutrient indication
				  62: pH indication
				  65: Sensitivity to eutrophication
					Forests
					  16: Forest or non-forest habitats
					  51: Functional group plants
					Shadiness
					  50: Shadiness growing habitat
					Humidity
					  17: Terrestrial humidity
					Wind
					  52b: Pollination wind
					  53a: Seed dispersal by wind

Species sensitivity	Quality change	Phenology
		  22: Reproductive period
		Dependency on other species
		  34: Depending on symbiosis
		  41a: Herbivores depending on one species
		  42a: Predators depending on one species
		  43a: Parasites depending on one species
		  63: Functional group fungi
			Dependency on other species
			  34: Depending on symbiosis
			  41a: Herbivores depending on one species
			  42a: Predators depending on one species
			  43a: Parasites depending on one species
			  63: Functional group fungi
				Human disturbance
				  3: Controlled by man
				  26: Considered a pest
				  27: In agricultural area before 1960
				  28: In agricultural area after 1960
					Dependency on other species
					  63: Functional group fungi

	Fragmentation		Dispersal ability
			  25: Dispersion capacity
			  45: Flying
			  46: Active dispersion
			  47: Passive dispersion
			  52: Pollination type
			  53: Dispersion of seeds
			Offspring
			  29: Number of generations per year
			  31: Years before reproduction
			  32: Reproductive years
			  48: Number of offspring per year
			  54: Seed longevity
			Abundance
			  10: Body size
			  36: Reproductive area		

the response variable (here decline) (Strobl et al., 2009). Moreover, since on every node it is decided which predictive variable should be used for dividing the remaining set of cases, interactions between predictive variables are also taken into consideration. These are important strengths of this approach over a variance-covariance approach like regression analyses. It makes classification tree-based approaches real non-parametric alternatives for regression-based approaches (Strobl et al., 2009). We used with the package '*party*' of R for calculating the random forests (R Development Core Team, 2015).

2.2.5. Assess importance of attributes

Using random forests, the importance of an attribute for the classification of species – here, declining or not declining - is estimated by comparing the proportion of correct classifications of the random forest with that of a random forest in which the values of that attribute are randomly permuted (Strobl et al., 2009). The decrease in correct classification is a measure of the importance of that attribute. However, it has been shown that this measure is biased towards correlated

attributes (Strobl et al., 2007). Therefore, the alternative measure of importance developed to solve this problem by conditional permutation, was used: the 'conditional importance' (Strobl et al., 2008). All default settings of *party* were kept, except for the number of attributes tested per node, which was set on the square root of the total number of attributes as recommended by Strobl et al. (2009).

We ensured robustness of the importance estimates and the ranking of attributes according to their importance by applying 100 random forests and calculating the median and 95th percentile of the importance. We have chosen median and percentiles, instead of mean and standard deviation, because we cannot assume importance is normally distributed (Fig. 3).

2.2.6. Assess importance per driver

The conditional importance of attributes with random values will have a median of zero (Strobl et al., 2009). As a result, a number of attributes will have a negative importance. The distribution of these negative values can be regarded as half of the variance distribution of

Fig. 3. Frequency distribution of the conditional importance of 87 attributes used in a conditional random forest to classify the vertebrates into species that decline and species that do not decline. 5% of the negative importance's are smaller than $-0.58 * 10^{-3}$. Therefore we regard all attributes having an importance of greater than $0.58 * 10^{-3}$ as greater than zero, i.e., non-zero. In this example, showing one random forest run for vertebrate species 19 attributes have a non-zero importance.
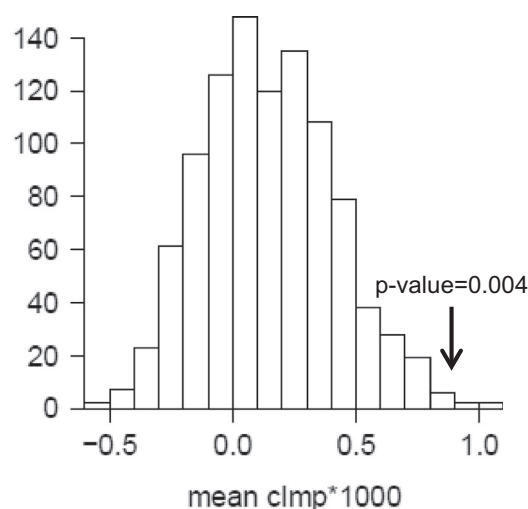

Fig. 4. Frequency distribution of the mean conditional importance of 1000 random samples of 10 fungi attributes. In one random forest run for the fungi species, the set of 10 attributes associated with climate change had a mean importance of $0.90 * 10^{-3}$. Only 4 random samples had a higher mean importance, resulting in a p-value for climate change attributes of 0.004.

attributes with random values. In accordance with Strobl et al. (2009), we use the negative variance distribution to calculate a threshold value for deciding which attributes have an importance of higher than zero. So, attributes that have a higher median importance than the 95% value of the negative variance distribution turned positive are regarded as having a higher importance than zero (Strobl et al., 2009). This approach is illustrated in Fig. 3, using the importance of one random forest of the vertebrates.

Our first metric for assessing the importance of a specific driver in explaining decline is the proportion of attributes with an importance higher than zero, called the non-zero attributes hereafter, associated with that driver. This metric was chosen for its robustness: if a driver affects the decline of species, we expect that at least some of the associated attributes will be non-zero, even if not all attribute-driver associations are equally strong. This metric is independent of the actual importance, which may be affected by the proximity of the attribute-decline association (even though the actual gradient of a driver is not needed for the analysis and hence cannot bias the results) or the heterogeneity within the group of species.

Our second metric is the mean importance of our set of attributes associated with an individual driver. This metric gives an estimate of the strength of the association between attributes and species decline, averaged over the attributes associated with a specific driver.

For each driver, we tested the performance of these metrics by comparing the proportion of non-zero attributes and the mean importance of the associated attribute sets vs. random sets containing an equal number of attributes. The random sets were created by $1000 \times$ bootstrapping (without replacement) this number of attributes from the complete set of attributes in the random forest of the species group. The proportion of non-zero attributes and the mean importance of random forests that were greater than or equal to the calculated proportion of non-zero attributes and the mean importance for a given driver equaled the corresponding one sided p-value. We calculated this p-value for 100 random forests to additionally obtain the distribution of p-values. Fig. 4 gives an example of the calculation of a p-value of climate change as a driver for decline in fungi. All calculations were done with R (R Development Core Team, 2015).

3. Results

Random forests of vertebrates, insects, plants and fungi correctly classified declining species on average (± sd) for, respectively, 60.0 ± 0.6, 66.1 ± 0.47, 67.0 ± 0.32, and 51.1 ± 1.10% of the species. Of the 87 attributes available, 21 and 35 had an importance greater than zero for vertebrate species and insects, respectively, compared with 13 out of 42 were non-zero for plants, and 3 out of 30 for fungi. Although the exact relationship between the attribute values and the decline of the species is not relevant for our approach - whenever an attribute is able to separate the declining from the not-declining species, it has an importance greater than zero - we show per species group how each of these non-zero attributes is related to the probability of species decline in Appendix D, Fig. D1 and Table D1.

We calculated the proportion of the associated attributes being non-zero and the probabilities of that proportion being equal to that of a random sample of attributes (Fig. 5; the same results, but ordered per species group, are in Appendix E, Fig. E1). It shows that climate change was an important driver (proportions well below 0.05 and hence significantly different from chance) only for fungi. In the case of fragmentation, they are well below 0.05 for vertebrates and below 0.10 for plants. In the case of agricultural change and reforestation about half of the probabilities are below 0.10 for vertebrates.

Figs. 6 and E2 present the mean importance of the associated attributes and the probabilities of that mean being at least equal to that of a random sample of attributes. For most combinations of driver and species group, this shows a similar pattern as the probabilities of the proportions. The mean importance of fragmentation attributes has p-values below 0.05 for insects and plants too. Agricultural intensification and reforestation have higher p-values for mean importance than for proportion of non-zero attributes.

4. Discussion

4.1. Attribute importance analysis (AIA)

The AIA is a novel, trait-based approach for analyzing species-environment relationships, in this case the relationship between species decline and environmental drivers. It is relatively simple and clear cut in comparison to previous, spatially explicit approaches (Fox et al., 2014; Bradshaw et al., 2015; Fraixedas et al., 2015). It does not depend on spatial gradients in the environmental drivers (and is thus not affected by different gradients among environmental drivers). However, because it is a novel approach, its performance demands extensive
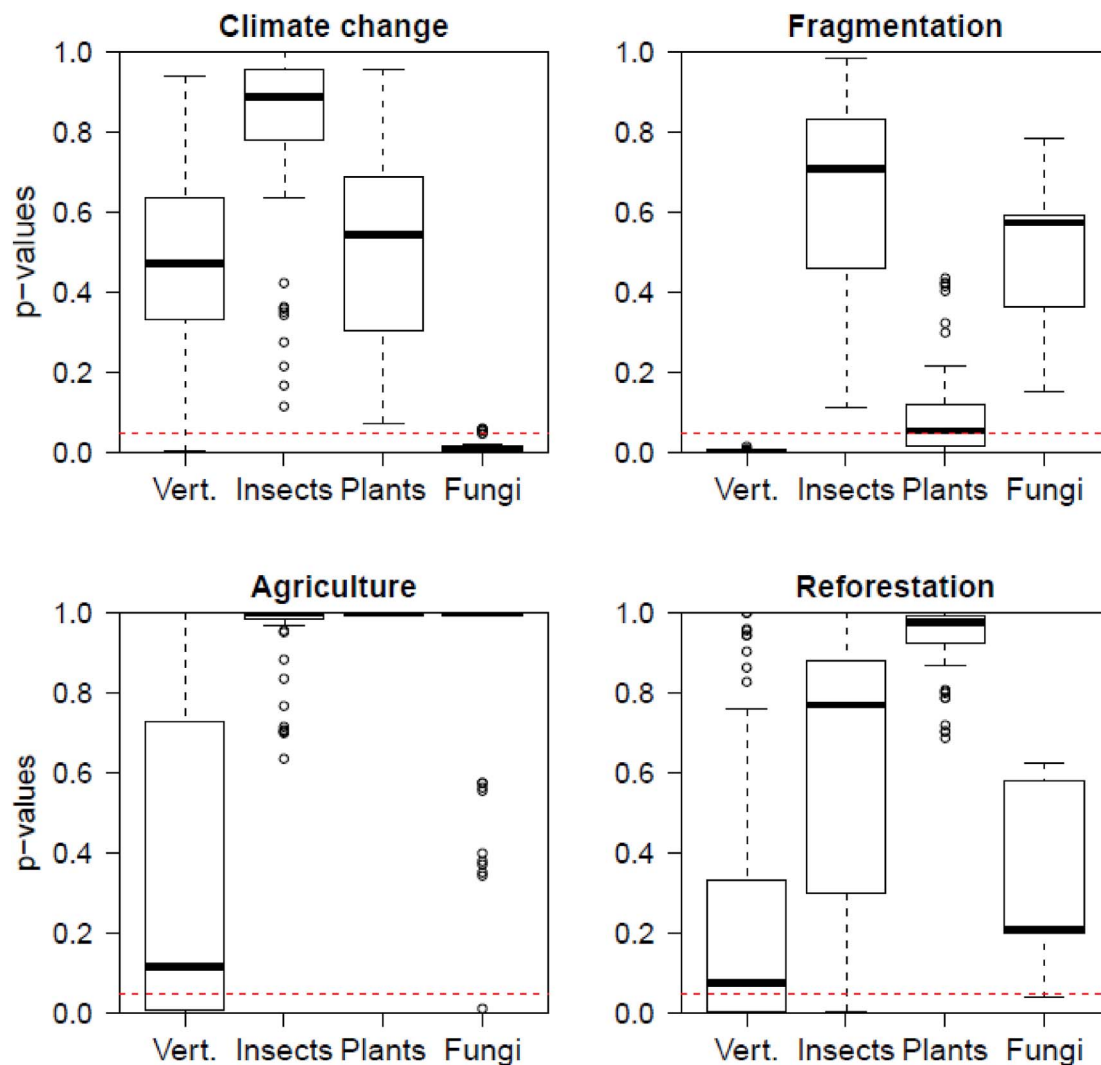
Fig. 5. Proportion of non-zero attributes associated with the four studied drivers of species decline. Distribution of the p-values of the proportion of non-zero attributes being higher than that proportion of a random selection of attributes per species group is given. Number of attributes associated with climate change are for vertebrates, insects, plants and fungi, resp. 16, 16, 13 and 10; with fragmentation, resp. 10, 10, 6 and 6; with agricultural intensification, resp. 11, 11, 11 and 10; and with reforestation, resp. 16, 16, 13 and 10. The thick horizontal line is the median p-value, 50% of all p-values are in the boxes, o are outliers. The dashed red line is at p-value = .05. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

evaluation and here we provide a proof of principle for the Netherlands, hoping that others may find our approach useful for answering their questions. Before going into the results of our proof of principle, we first discuss the potential weaknesses of the approach and our solutions.

A crucial step in AIA, as in any trait-based approach on the relationship between biodiversity change and environmental drivers, is the selection of attributes (Estrada et al., 2016; Moretti et al., 2017). First, it can be argued that not all important attributes that determine the possibilities of species to cope with specific drivers may have been included. For instance, metabolic attributes could be associated with climate change or agricultural intensification, but were not included because of lack of information on these attributes. Second, not all attributes associated with a particular driver may have a strong, direct response to that driver, i.e., some attributes associated to a driver may be under weak selection by the driver. In our analysis, these attributes would have a low importance even though the driver is the actual cause of decline and the distribution of the attribute values in the community will in the long run be changed by the driver. This might be especially problematic for the interpretation of the results when one or more of the drivers have all their selected associated attributes belonging to this type. Third, some attributes could be responsive to more than one cause

of decline. Attributes that enable species to cope with change in general are related to all environmental drivers (and were not included in our analysis).

Since these problems of attribute selection are common to many trait-based studies – the first two form a problem in any study on the relative importance of attribute values for species survival (e.g., the references in Appendix C), the third in any study on the relative importance of environmental drivers for attribute-dependent species survival. This points to an urgent need for better procedures for attribute selection and more knowledge on the relationship between attribute values and species trends as well as the limitations of trait-based studies. Recently some progress has been made in this field, mainly focusing on standardizing trait definition and measurement (Estrada et al., 2016; Moretti et al., 2017; Garnier et al., 2017) and on the relationship between specific drivers, attributes, and species trends (Bregman et al., 2017; Siepielski et al., 2017; Bowler et al., 2017; van Strien et al., 2017; Pöyry et al., 2017).

Another type of problem is that species groups may be ecologically so heterogeneous that decline of some species within the group relate to other attributes than that of other species. Decision trees are especially fit for finding the attributes that predict the decline in subgroups, but,
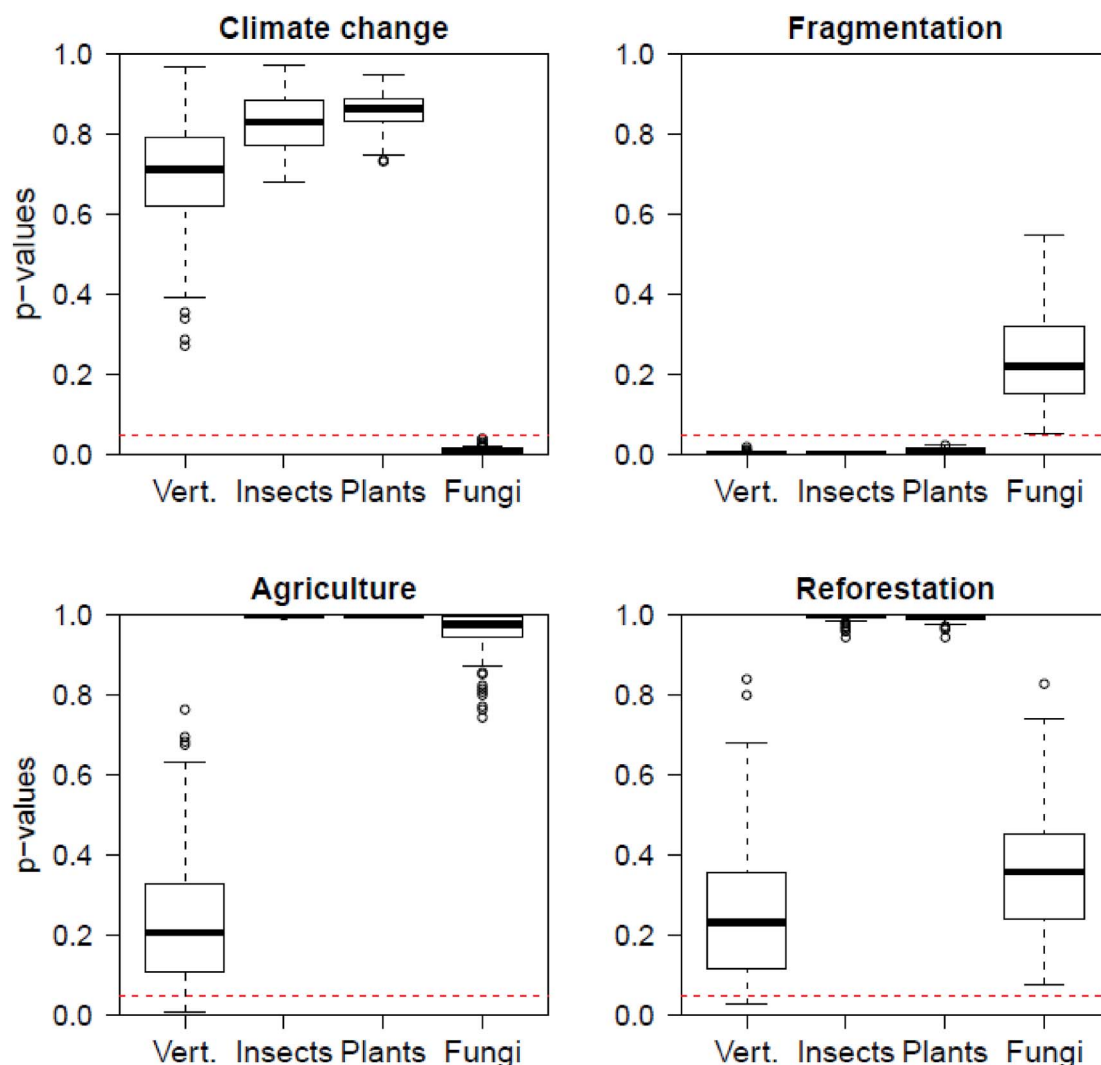
Fig. 6. Mean importance of attributes associated with the four studied drivers of species decline. Distribution of the p-values of the mean importance of the associated attributes being higher than the mean importance of a random selection of attributes per species group is given. Number of attributes associated with climate change are for vertebrates, insects, plants and fungi, resp. 16, 16, 13 and 10; with fragmentation, resp. 10, 10, 6 and 6; with agricultural intensification, resp. 11, 11, 11 and 10; and with reforestation, resp. 16, 16, 13 and 10. The thick horizontal line is the median p-value, 50% of all p-values are in the boxes, o are outliers. The dashed red line is at p-value = .05. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

depending on the size of the subgroups and the predictive power of the attributes, the associated attributes may show relatively low importance in such cases. The obvious solution for this problem is to split the species group into more ecological homogeneous groups, for example in aquatic and terrestrial species. However, this splitting may be in conflict with the goal of a study to find general strategies for the conservation policy at the level of, say, countries or regions.

In this study, AIA has been made robust against the problems of selecting attributes per driver by, first of all, including a long list of attributes to start with and selecting never fewer than 6 and usually more than 10 associated attributes per driver, so that our analyses never depend on one or two attributes only. Second, we chose to allow attributes to be associated to more than one driver, as long as an attribute was not associated with all four drivers. This was done to ensure that any signal of the effect of a driver was included in the two metrics. Third, because selecting only those attributes that are known to have a strong responsive relationship with the driver is impossible due to the sparse literature on the subject (Appendix C), we used two testing metrics, the proportion of non-zero attributes and the mean importance. Because the first metric ignores the value of the importance, it is robust against the problem of the relative strength of the relationship

between attribute and driver. It is also robust against the problem of group heterogeneity that can cause low importance of attributes that are only predictive for a small part of the species within the species group. However, it is insensitive to the actual explanatory power of the attributes. For that we have the mean importance. Our results on insects vs. fragmentation show the relevance of studying both testing metrics (see below).

The AIA as proposed here is based on the calculation of the attributes' importance using random forests. In theory, it could also have been done based on logistic regression analyses (e.g., Angert et al., 2011; van Bodegom et al., 2014). However, because of the large number of attributes, the number of parameters in regression analyses would be so large in relation to the number of species that the probability of spurious results would have been substantial, if an analysis would be possible at all (Anderson, 2008; Strobl et al., 2009). Several studies have compared the performance of decision tree with multiple regression for analyzing complex ecological data and found that the first were adequate if not superior to the last (e.g., De'ath and Fabricius, 2000; Prasad et al., 2006; Williams et al., 2009; Hegel et al., 2010; Oliveira et al., 2012; Delgado et al., 2014).

Overall, we think that our AIA is robust and could deliver solid

results. Even so, it should not be forgotten that in the end AIA cannot *prove* causal relationships. Its strength lies in its a priori approach, its potential of handling a large number of predictive variables and its robustness because of its low dependency on statistical assumptions. But, obviously, the quality of its results depends also on the quality of the data, i.e., on adequate information on the decline and attribute values of the species, on inclusion of all relevant attributes, and on correct association of attributes with drivers. Our information on decline of species can be regarded as solid (A. van Strien, *in lit.*), but the inclusion of all relevant attributes, the assessment of attribute values per species and the correct association of attributes with drivers depended partly on expert judgments. The following discussion of the results should therefore be regarded as preliminary and mainly for generating hypotheses.

4.2. Causes of decline

Both our metrics, proportion of non-zero attributes and mean importance, show that the attributes associated with climate change explained the decline of fungi, but not the decline of the other species groups in the Netherlands. Our metrics also show that attributes associated with fragmentation explained the decline of vertebrates and plants, and maybe insects in the Netherlands. Both metrics show also that the attributes associated with agricultural intensification only explained the decline of vertebrates in part of our 100 random forests. Likewise, in some random forests only, attributes associated with reforestation related to the decline of vertebrate species.

Although climate change is a well-recognized cause of projected population changes and presents changes in phenology and range shifts (e.g., Visser et al., 1998; Foden et al., 2013; Elmhagen et al., 2015b; Kullberg et al., 2015; Kerr et al., 2015; Hovick et al., 2016), it was in the MEA (2005) regarded as having a low impact on biodiversity over the last century. Our results for the Netherlands seem to confirm this, except for fungi, a group that is showing effects of climate change, probably due to the fact that these are narrowly restricted to certain temperature-humidity combinations for fruiting (Kauserud et al., 2008). Of course, a decline in fruiting bodies does not necessary reflect a decline in populations size of the fungi. Further, it should be noted that of all 30 attributes of fungi, only three were non-zero, and the predictive power of the random forests was relatively low (51.1% of the species correctly classified).

Concerning the impacts of fragmentation on the decline in vertebrates, plants and fungi, our analyses identify fragmentation as clearly the most important cause of species decline for vertebrates and plants, but not for fungi, in the Netherlands. The impact of fragmentation on vertebrates has been shown in several papers (e.g., Haddad et al., 2015; Blandón et al., 2016). Likewise, the impact of fragmentation on plants confirms earlier research that identified colonization ability to be crucial for local plant survival (Blomqvist et al., 2003; Ozinga et al., 2009; Evju et al., 2015; Haddad et al., 2015). Our hypothesis is that isolation is the key factor for the impact, although it may also concern lagged decline caused by habitat loss in earlier periods (Haddad et al., 2015) or changes in habitat quality, e.g. due to nitrogen deposition. That fragmentation may not be an important driver of decline for fungi is not surprising, since most fungi in our analysis are mushrooms that can easily overcome barriers by their spores.

For insects, the assessment of fragmentation impacts on species decline was not consistent across metrics. The proportion of non-zero attributes was not higher than that of a random sample of attributes, but the mean importance was. This is due to the attribute 'Active dispersion' that distinguishes short distance dispersers from long distance dispersers. This attribute has a very high importance (Fig. D1, Table D1). Dropping this attribute from our analysis reduces the mean importance for insects below the level of being significantly higher than expected (Appendix F, Fig. F1). Hence, we have found only one attribute to support that insect decline is related to fragmentation, which

seems weak as support. In aquatic systems, it has been shown that small organisms are less strongly affected by isolation than larger organisms and that flying insects are even less affected than other organisms of the same size class (de Bie et al., 2012). If this is a general pattern, it would mean that vertebrates should be more strongly affected by fragmentation than insects (but also see Haddad et al., 2015), which is supported by our results on the proportion of non-zero attributes (Fig. 5). On the other hand, the attribute 'Active dispersion' seems to have a very direct relationship to fragmentation and its predictive power is really high (Fig. D1). Obviously, more research is needed here.

Reforestation showed consistent results over the two metrics and does not seem of great importance for any group of species, although there is a weak signal of importance for vertebrates in our results. In general, forest species, which in the Netherlands are often species that live both in woodlands and urban parks, seems to do well (CBS, PBL, and Wageningen UR, 2015), but reforestation may be a too recent development to be visible in the species trends since the 1950s.

The most unexpected result is the consistent unimportance of agricultural intensification as a cause of species decline, except for a weak signal in vertebrates. One could have expected this importance to be greater since most studies into the cause of change of biodiversity in the Netherlands, and Europe in general, identify agriculture as a key driver (e.g., Stoate et al., 2009; Geiger et al., 2010; Wamelink et al., 2013). A possible reason might be that the Dutch species are species that have survived the strong intensification of agriculture that took place at the end of the 19th and the beginning of the 20th century. For these species, the relatively small changes from highly intensive to mega-intensive agriculture, that occurred since the fifties, may be of less importance. This is suggested by the fact that the most rapid decrease of pollinators occurred before WWII in Britain (Ollerton et al., 2014). If this is true, then the actual mechanism of agricultural change as a driver of change of populations is the isolation of natural habitat and not so much the loss of quality within agricultural systems, which disappeared much earlier. Isolation of natural habitat is captured by 'fragmentation' in our analysis. The partitioning of the effects of agriculture on biodiversity into the effects of intensification and the effects of isolation need further study because the results might have important policy implications (Green et al., 2005; Phalan et al., 2011).

The proportion of non-zero attributes of agricultural intensification in vertebrates was highly variable, ranging from 0 to 1 (Fig. 5). This high variance seems to indicate that many of the attributes had an importance close to the threshold value, causing a high variation in the proportion of non-zero attributes for agriculture. This supports our interpretation that there is only a weak support of the hypothesis that the decline of vertebrates is affected by agricultural intensification.

4.3. Policy implications

Our results support the idea that, except for fungi, the decline of species since WWII in the Netherlands has been caused by land use change, in particular fragmentation, rather than climate change. Of course, in other countries or regions different drivers might be important because of different climate, geology or land use history.

Our results would mean that nature conservation measures for biodiversity in the Netherlands in general - not for specific species - should have been concentrated on defragmentation. Defragmentation can be obtained by restoring natural habitats and connecting old and new nature conservation areas. This strategy has in fact been the main nature conservation strategy in the Netherlands since 1990 (realization of the Ecological Main Structure) and has also been adopted in the EU in the Natura 2000 strategy (http://ec.europa.eu/environment/nature/natura2000/). Whether this strategy should be continued cannot be concluded from our analyses, but based on a scenario study, Lehsten et al. (2015) concluded recently that mitigation actions for conserving European habitats should keep on focusing on land use change rather than climate change.

Along with this focus on nature conservation areas, since 1975 there has also been a strategy to mitigate agricultural intensification in the form of Agri-Environmental Schemes (AES, in the EU since 1985, Batáry et al., 2015). AES are presently under discussion in the Netherlands because of their disappointing results so far (Kleijn, 2012). Batáry et al. (2015) found that schemes that take out areas from agricultural production have been more effective than schemes that tried to change production. Our results support the idea that mitigation of land use intensity may not have been a very promising general strategy for biodiversity conservation in the Netherlands.

Authors' contributions

Both authors conceived the ideas and designed methodology; CM collected and analyzed the data; he also wrote the manuscript; PvB contributed critically to drafts and both authors gave final approval for publication.

Acknowledgement

Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.01.002.

References

Anderson, D.R., 2008. Model Based Inference in the Life Sciences. A Primer on Evidence. Springer, New York.

Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J., Chunco, A.J., 2011. Do species' traits predict recent shifts at expanding range edges? Ecol. Lett. 14, 677–689.

Batáry, P., Dicks, L.V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environmental schemes in conservation and environmental management. Conserv. Biol. 29, 1006–1016.

de Bie, T., De Meester, L., Brendonck, L., et al., 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecol. Lett. 15, 740–747.

Blandón, A.C., Perelman, S.B., Ramírez, M., López, A., Javier, O., Robbins, C.S., 2016. Temporal bird community dynamics are strongly affected by landscape fragmentation in a Central American tropical forest region. Biodivers. Conserv. 25, 311–330.

Blomqvist, M.M., Vos, P., Klinkhamer, P.G.L., ter Keurs, W.J., 2003. Declining plant species richness of grassland ditch banks - a problem of colonisation or extinction? Biol. Conserv. 109, 391–406.

van Bodegom, P.M., Douma, J.C., Verheijen, L.M., 2014. A fully traits-based approach to modeling global vegetation distribution. PNAS 111, 13733–13738.

Bowler, D.E., Hof, C., Haase, P., et al., 2017. Cross-realm assessment of climate change impacts on species' abundance trends. Nat. Ecol. Evol. 1, 0067.

Bradshaw, C.J.A., Brook, B.W., Delean, S., et al., 2015. Predictors of contraction and expansion of area of occupancy for British birds. Proc. R. Soc. B 281, 20140744.

Bregman, T.P., Lees, A.C., MacGrego, H.E.A., et al., 2017. Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. Proc. R. Soc. B 283, 20161289.

Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32.

CBS, PBL, Wageningen UR, 2008. Areaalverandering van duinbiotopen (indicator 1122, versie 02, 24 april 2008). www.compendiumvoordeleefomgeving.nl (CBS, Den Haag; Planbureau voor de Leefomgeving, Den Haag/Bilthoven en Wageningen UR, Wageningen).

CBS, PBL, Wageningen UR, 2013. Bodemgebruik, 1900–2008 (indicator 1001, versie 07, 22 augustus 2013). www.compendiumvoordeleefomgeving.nl (CBS, Den Haag; Planbureau voor de Leefomgeving, Den Haag/Bilthoven en Wageningen UR, Wageningen).

CBS, PBL, Wageningen UR, 2014. Inleiding natuur en milieu (indicator 1091, versie 05, 24 januari 2014) & Areaal bostypen 1984–2013 (indicator 1160, versie 07, 23 juli 2014). CBS, Den Haag; Planbureau voor de Leefomgeving, Den Haag/Bilthoven en Wageningen UR, Wageningen.

CBS, PBL, Wageningen UR, 2015. Flora van naaldbossen, 1999–2014 (indicator 1545, versie 05, 15 december 2015) & Flora van loof- en gemengde bossen, 1999–2014 (indicator 1546, versie 05, 11 december 2015) & Trend fauna in bossen, 1990–2014 (indicator 1162, versie 13, 29 oktober 2015) & Vogels van oude bossen op hogere zandgronden, 1990–2012 (indicator 1170, versie 12, 8 januari 2014). www.

compendiumvoordeleefomgeving.nl (CBS, Den Haag; Planbureau voor de Leefomgeving, Den Haag/Bilthoven en Wageningen UR, Wageningen).

De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178–3192.

Delgado, M.F., Cernadas, E., Barro, S., 2014. Do we need hundreds of classifiers to solve real world classification problems? J. Mach. Learn. Res. 15, 3133–3181.

Deng, H., Runger, G., Tuv, E., 2011. Bias of importance measures for multi-valued attributes and solutions. In: Proceedings of the 21st International Conference on Artificial Neural Networks, pp. 1–9.

Dingemans, N.J., Kalkman, V.J., 2008. Changing temperature regimes have advanced the phenology of Odonata in the Netherlands. Ecol. Entomol. http://dx.doi.org/10.1111/j.1365-2311.2007.00982.x.

Elmhagen, B., Eriksson, O., Lindborg, R., 2015a. Implications of climate and land-use change for landscape processes, biodiversity, ecosystem services, and governance. Ambio 44 (Suppl. 1), S1–S5.

Elmhagen, B., Kindberg, J., Hellström, P., Angerbjörn, A., 2015b. A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. Ambio 44 (Suppl. 1), S39–S50.

Estrada, A., Morales-Castilla, I., Caplat, P., Early, R., 2016. Usefulness of species traits in predicting range shifts. Trends Ecol. Evol. 31, 190–203.

Evju, M., Blumentrath, S., Skarpaas, O., Stabbetorp, O.E., Sverdrup-Thygeson, A., 2015. Plant species occurence in a fragmented grassland landscape: the importance of species traits. Biodivers. Conserv. 24, 547–561.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515.

Foden, W.B., Butchart, S.H.M., Stuart, S.N., et al., 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. PLoS One 8, e65427.

Fox, R., Oliver, T.H., Harrower, C., Parsons, M.S., Thomas, C.D., Roy, D.B., 2014. Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. J. Appl. Ecol. 51, 949–957.

Fraixedas, S., Lehikoinen, A., Lindén, A., 2015. Impact of climate and land use change on wintering bird populations in Finland. J. Avian Biol. 46, 63–72.

Garnier, E., Stahl, U., Laporte, M.-A., 2017. Towards a thesaurus of plant characteristics: an ecological contribution. J. Ecol. 105, 298–309.

Geiger, F., de Snoo, G.R., Berendse, F., et al., 2010. Landscape composition influences farm management effects on farmland birds in winter: a pan-European approach. Agric. Ecosyst. Environ. 130, 571–577.

Green, R.E., Cornell, S.J., Scharlemann, J.P., Balmford, A., 2005. Farming and the fate of wild nature. Science 307, 550–555.

Haddad, N.M., Brudvig, L.A., Clobert, J., et al., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1, e1500052.

Hegel, T.M., Cushman, S.A., Evans, J., Huettmann, F., 2010. Current state of the art for statistical modelling pf species distributions. In: Cushman, S.A., Huettmann, F. (Eds.), Spacial Complexity, Informatics, and Wildlife Conservation. Springer, Tokyo, pp. 273–311.

Hovick, T.J., Allred, B.W., McGranahan, D.A., Palmer, M.W., Elmore, R.D., Fuhlendorf, S.D., 2016. Informing conservation by identifying range shift pattern across breeding habitats and migration strategies. Biodivers. Conserv. 25, 345–356.

de Iongh, H.H., Bal, D., 2007. Harmonization of Red Lists in Europe: some lessons learned in the Netherlands when applying the new IUCN Red List Categories and Criteria version 3.1. Endanger. Species Res. 3, 53–60.

Kalkman, V.J., van Duuren, L., Gmelig Meyling, A.W., Odé, B., 2010. Veranderingen in de Nederlandse biodiversiteit. In: Noordijk, J., Kleukers, R.M.J.C., van Nieuwkerken, E.J., van Loon, A.J. (Eds.), De Nederlandse biodiversiteit. Nederlandse Fauna 10. Nederlands Centrum voor Biodiversiteit Naturalis & European Invertebrate Survey, Leiden, pp. 339–354.

Kauserud, H., Stige, L.C., Vik, J.O., Økland, R.H., Høiland, K., Stenseth, N.C., 2008. Mushroom fruiting and climate change. PNAS 105, 3811–3814.

Kerr, J.T., Pindar, A., Galpern, P., et al., 2015. Climate change impacts on bumblebees converge across continents. Science 349, 177–180.

Kleijn, D., 2012. De effectiviteit van Agrarisch Natuurbeheer. Alterra, Wageningen. http://www.rli.nl/sites/default/files/u61/david_kleijn_-_de_effectiviteit_van_agrarisch_natuurbeheer.pdf.

Kleukers, R., Reemer, M., 2003. Verandering in de Nederlandse ongewervelden fauna. De Levende Natuur. vol. 104. pp. 86–89.

Kullberg, C., Fransson, T., Hedlund, J., Jonzén, N., Langvall, O., Nilsson, J., Bolmgren, K., 2015. Change in spring arrival of migratory birds under an era of climate change, Swedish data from the last 140 years. Ambio 44 (Suppl. 1), S69–S77.

Lehsten, V., Sykes, M.T., Scott, A.V., et al., 2015. Disentangling the effects of land-use change, climate and CO_2 on projected future European habitat types. Glob. Ecol. Biogeogr. 24, 653–663.

Luoto, M., Virkkala, R., Heikkinen, 2007. The role of land cover in bioclimatic models depends on spatial resolution. Glob. Ecol. Biogeogr. 16, 34–42.

MEA, 2005. Millennium Ecosystem Assessment. Ecosystems and Human Well-being: Synthesis. Island Press, Washington, DC.

Moretti, M., Dias, A.T.C., de Bello, F., et al., 2017. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. Funct. Ecol. 31, 558–567.

Mouillot, D., Graham, N.A.J., Villéger, S., Norman, W.H., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28, 167–177.

Murray, K.A., Rosauer, D., McCallum, H., Skerratt, L.F., 2011. Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. Proc. R. Soc. B 278, 1515–1523.

Musters, C.J.M., ter Keurs, W.J., de Snoo, G.R., 2010. Timing of the breeding season of

Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* in The Netherlands. Ardea 98, 195–202.

Musters, C.J.M., Kalkman, V., van Strien, A., 2013. Predicting rarity and decline in animals, plants, and mushrooms based on species attributes and indicator groups. Ecol. Evol. 3, 3401–3414.

van Nieuwkerken, E.J., van Loon, A.J., 2010. In: Noordijk, J., Kleukers, R.M.J.C. (Eds.), De Nederlandse biodiversiteit. Nederlandse Fauna 10. Nederlands Centrum voor Biodiversiteit Naturalis & European Invertebrate Survey, Leiden.

Oliveira, S., Oehler, F., San-Miguel-Ayanz, J., Camia, A., Periera, J.M.C., 2012. Modeling spatial patterns of fire occurrence in Mediterranean Europe using multiple regression and random forest. For. Ecol. Manag. 275, 117–129.

Ollerton, J., Erenler, H., Edwards, M., Crockett, R., 2014. Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. Science 346, 1360–1362.

Ozinga, W.A., Romermann, C., Bekker, R.M., et al., 2009. Dispersal failure contributes to plant losses in NW Europe. Ecol. Lett. 12, 66–74.

Phalan, B., Onial, M., Balmford, A., Green, R.E., 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. Science 333, 1289–1291.

Pöyry, J., Carvalheiro, L.G., Heikkinen, R.K., et al., 2017. The effects of soil eutrofication propagate to higher trophic levels. Glob. Ecol. Biogeogr. 26, 18–30.

Prasad, A.M., Iverson, L.R., Liaw, A., 2006. Newer classification and regression tree techniques: bagging and random forests for ecological prediction. Ecosystems 9, 181–199.

R Development Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Dtatistical Computing, Vienna. http://www.R-project.org.

Siepielski, A.M., Morrissey, M.B., Buoro, M., et al., 2017. Precipitation drives global variation in natural selection. Science 355, 959–962.

Stoate, C., Báldi, A., Beja, P., et al., 2009. Ecological impacts of early 21st century agricultural change in Europe. J. Environ. Manag. 91, 22–46.

van Strien, A.J., Boomsluiter, M., Noordeloos, M.E., et al., 2017. Woodland ectomy-corrizal fungi benetit from large-scale reduction in nitrogen deposition in the Netherlands. J. Appl. Ecol. http://dx.doi.org/10.1111/1365-2664.12944.

Strobl, C., Boulesteix, A.-L., Zeileis, A., Hothorn, T., 2007. Bias in random forest variable importance measures: illustrations, sources and a solution. BMC Bioinf. 8, 25.

Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T., Zeileis, A., 2008. Conditional variable importance for random forests. BMC Bioinf. 9, 307.

Strobl, C., Malley, J., Tutz, G., 2009. An introduction to recursive partitioning: rationale, application, and characteristics of classification and regression trees, bagging, and random forests. Psychol. Methods 14, 323–348.

Tamis, W.W.L.M., Duistermaat, L.H., van Moorsel, R.R.C.M.J., 2009. Het verdwijnen en (weer) verschijnen van plantensoorten in Nederland. Gorteria 33, 166–185.

Urban, M.C., 2015. Accelerating extinction risk from climate change. Science 348, 571–573.

Vellend, M., 2016. The theory of ecological communities. In: Monographs in Population Biology 57. Princeton University Press, Princeton and Oxford.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional!. Oikos 116, 882–892.

Visser, M.E., Both, C., 2005. Shifts in phenology due to global climate change: the need for a yardstick. Proc. R. Soc. B 272, 2561–2569.

Visser, M.E., van Noordwijk, A.J., Tinbergen, J.M., Lessells, C.M., 1998. Warmer springs lead to mistimed reproduction in great tits. Proc. R. Soc. Lond. B 265, 1867–1870.

Wamelink, G.W.W., de Knegt, B., Pouwels, R., et al., 2013. Considerable environmental bottlenecks for species listed in the Habitats and Birds Directives in the Netherlands. Biol. Conserv. 165, 43–53.

Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I., Poff, N.L., 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecol. Lett. 13, 267–283.

Wereld Natuur Fonds, 2015. Living Planet Report. Natuur in Nederland. WNF, Zeist.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., Langham, G., 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biol. 6, 2621–2626.

Williams, J.N., Seo, C., Thorne, J., Nelson, J.K., Erwin, S., O'Brien, J.M., Schwartz, M.W., 2009. Using species distribution models to predict new occurrences of rare plants. Divers. Distrib. 15, 565–576.